

Utah State University

DigitalCommons@USU

All Graduate Theses and Dissertations

Graduate Studies

5-1980

Carbon Isotope Ratios of Soil Organic Matter and Their Use in Assessing Community Composition Changes in Curlew Valley, Utah

Ronald S. Dzurec
Utah State University

Follow this and additional works at: <https://digitalcommons.usu.edu/etd>



Part of the [Life Sciences Commons](#)

Recommended Citation

Dzurec, Ronald S., "Carbon Isotope Ratios of Soil Organic Matter and Their Use in Assessing Community Composition Changes in Curlew Valley, Utah" (1980). *All Graduate Theses and Dissertations*. 3444.
<https://digitalcommons.usu.edu/etd/3444>

This Thesis is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.



CARBON ISOTOPE RATIOS OF SOIL ORGANIC MATTER
AND THEIR USE IN ASSESSING COMMUNITY
COMPOSITION CHANGES IN
CURLEW VALLEY, UTAH

by
Ronald S. Dzurec

A thesis submitted in partial fulfillment
of the requirements for the degree

of
MASTER OF SCIENCE
in
Range Ecology

UTAH STATE UNIVERSITY
Logan, Utah
1980

ACKNOWLEDGEMENTS

278.2
D999c
c.2

Funding for this project was provided in part by the Utah Agricultural Experiment Station and the Graduate School of Utah State University.

A special note of thanks is extended to my major professor, Dr. Martyn Caldwell, who provided unending expertise and encouragement during all phases of my work. I would like to extend my appreciation to Dr. Neil West and Dr. Ben Norton for their assistance not only as committee members but as people whom I always felt free to approach on any matter. The assistance of Dr. John Skujins in introducing me to the pertinent soil literature and his thorough reviews of this thesis is gratefully acknowledged.

Three people from Brigham Young University provided a great deal of help during this project. Dr. Bruce Smith provided me with the unrestricted use of his mass spectrometry laboratory. Glen Martin furnished the technical assistance necessary to maintain the mass spectrometer. Dr. Thomas Boutton instructed me in the principles of sample preparation and mass spectrometry and provided me with lodging during my frequent forays to Provo. Without his help and friendship this project would have been impossible.

Finally, my deepest thanks go to my wife, Susan, and my son, Matthew, who made this work worth while. Susan's endless sacrifices during this time have served to deepen my love and respect for her. I dedicate this work to her.

Ronald S. Dzurec

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS.....	ii
LIST OF TABLES.....	iv
LIST OF FIGURES.....	v
ABSTRACT.....	vi
INTRODUCTION.....	1
METHODS.....	19
RESULTS.....	23
DISCUSSION.....	38
LITERATURE CITED.....	47
APPENDIXES.....	55
APPENDIX A. Carbon isotope ratios of samples from transect #2.....	56
APPENDIX B. Carbon isotope ratios of samples from transect #3.....	58

LIST OF TABLES

Table	Page
1. $\delta^{13}\text{C}$ values of litter, roots and soils from transect #1. Sample combustions and isotope determinations have a combined standard deviation of 0.1 o/oo. Vegetation cover key is: W=winterfat, S= shadscale and W/S= mixed winterfat and shadscale.....	26
2. $\delta^{13}\text{C}$ values of roots and soils from the supplementary cores. Sample combustions and isotope determinations have a combined standard deviation of 0.1 o/oo. Vegetation cover key is: W= winterfat and S= shadscale.....	35
3. $\delta^{13}\text{C}$ values of soil organic matter fractions. Both cores are from areas of winterfat dominance. Bulk soil represents soil prior to fractionation.....	37
4. $\delta^{13}\text{C}$ values of litter, roots and soils from transect #2. Sample combustions and isotope determinations have a combined standard deviation of 0.1 o/oo. Vegetation cover key is: W= winterfat, S= shadscale and W/S= mixed winterfat and shadscale.....	57
5. $\delta^{13}\text{C}$ values of litter, roots and soils from transect #3. Sample combustions and isotope determinations have a combined standard deviation of 0.1 o/oo. Vegetation cover key is: W= winterfat, S= shadscale and W/S= mixed winterfat and shadscale.....	59

LIST OF FIGURES

Figure	Page
1. Summary of climatic variation in the northeastern Great Basin during the Holocene. Authors and interpretations are given in the text. Blank areas represent a climate similar to the present. Stippled areas represent periods of greater effective moisture. The density of stippling is proportional to the amount of effective moisture above present levels.....	15
2. Photographs of the three transects analyzed in the study.....	24
3. Map of the dominant vegetation and sample locations at the study site in Curlew Valley, Utah. Areas where both winterfat and shadscale occur are indicated by stippling. Map coordinates are R.2 W, T.12N, section 15, Salt Lake City meridian.....	25
4. Carbon isotope ratios of litter (▲), roots (●) and soils (○) in relation to relative C_3/C_4 cover along transect #1. Soil and root values are the mean of at least three determinations. Error bars represent \pm one standard deviation.....	28
5. Carbon isotope ratios of litter (▲), roots (●) and soils (○) in relation to relative C_3/C_4 cover along transect #2. Soil and root values are the mean of at least three determinations. Error bars represent \pm one standard deviation.....	31
6. Carbon isotope ratios of litter (▲), roots (●) and soils (○) in relation to relative C_3/C_4 cover along transect #3. Soil and root values are the mean of at least three determinations. Error bars represent \pm one standard deviation.....	32
7. Photograph of a winterfat-dominated area from transect #3. A dead shadscale is behind the stake.....	33

ABSTRACT

Carbon isotope ratios of soil organic matter and
their use in assessing community composition changes
in Curlew Valley, Utah

by

Ronald S. Dzurec, Master of Science

Utah State University, 1980

Major Professor: Martyn M. Caldwell
Department: Range Science

Stable carbon isotope ratios of soils, roots and litter along transects stretching from nearly monospecific stands of Ceratoides lanata, a species possessing C_3 photosynthesis, to nearly monospecific stands of Atriplex confertifolia, a species possessing C_4 photosynthesis, were analyzed to determine if changes in the relative dominance of the shrubs have occurred in salt-desert communities. The $\delta^{13}C$ value, which reflects the proportion of ^{12}C and ^{13}C in a sample of plant tissue, can be used to distinguish between C_3 and C_4 species. Atriplex confertifolia and Ceratoides lanata have $\delta^{13}C$ values of -13.0 o/oo and -25 o/oo, respectively. The $\delta^{13}C$ value of litter and roots was used as a measure of current community dominance. The $\delta^{13}C$ value of soil organic matter was employed as a measure of past community dominance. The differential between $\delta^{13}C$ values of roots and soils was consistently about 3.0 o/oo in Ceratoides-dominated stands. Root $\delta^{13}C$ values were always more negative than soil $\delta^{13}C$ values. The striking uniformity in the root-soil $\delta^{13}C$ differential in Ceratoides-dominated stands is most likely the result of fractionation of carbon isotopes during decomposition.

The differential between $\delta^{13}\text{C}$ values of roots and soils in Atriplex-dominated stands was more variable. This most likely indicates a lack of long-term community stability in areas now dominated by Atriplex. In addition some samples of soil carbon from Atriplex-dominated stands had $\delta^{13}\text{C}$ values more negative than root $\delta^{13}\text{C}$ values. This suggests the presence of C_3 -derived carbon in areas currently dominated by the C_4 species Atriplex. These trends indicate that Atriplex has been increasing in importance in this salt-desert community.

The distribution of $\delta^{13}\text{C}$ values in relation to depth and among soil organic matter fractions was also studied. There was a trend for $\delta^{13}\text{C}$ values to become slightly less negative with depth. The $\delta^{13}\text{C}$ value of humic acid was most similar to the $\delta^{13}\text{C}$ value of the dominant vegetation. Fulvic acid was isotopically heavier than humic acid in all analyses. The implications of these trends are discussed.

(66 pages)

INTRODUCTION

The salt-desert shrub ecosystem type occupies nearly 100 million hectares in the western United States (Branson et al., 1967), principally within the physiographic confines of the Great Basin. It is a cold winter ecosystem type characterized by the development of extreme physiologic drought during the growing season. Precipitation is generally less than 250 mm per year with a considerable proportion of this occurring as snow during the dormant winter period. The salt-desert ecosystem type is best developed on saline valley bottoms throughout the Intermountain West and osmotic potentials as low as -35 bars have been reported for these halomorphic soils (Moore and Caldwell, 1972). The widespread dominance of this ecosystem type on such saline soils has led some to consider its plant communities as edaphic climaxes (Cronquist et al., 1972).

The plant communities are physiognomically dominated by shrubs. Atriplex confertifolia or shadscale, a member of a widely distributed and rapidly evolving genus (Stutz, 1978), is the principal dominant in upland sites. Ceratoides lanata or winterfat, the only known species in this genus, also occurs throughout the Intermountain West and in many areas achieves local dominance. Other important shrub species include Artemisia spinescens, Atriplex canescens, Atriplex gardneri, Atriplex nuttallii, Chrysothamnus viscidiflorus, Grayia spinosa, Gutierrezia sarothrae, Kochia americana, Lycium cooperi, Sarcobatus baileyi, Sarcobatus vermiculatus, and Tetradymia glabrata (Cronquist et al., 1972). These species generally occur as widely spaced individuals although in some areas they may achieve a high degree of cover.

Both Atriplex confertifolia and Ceratoides lanata are members of

the Chenopodiaceae family. This family contains both the C_3 and C_4 photosynthetic pathway (Welkie and Caldwell, 1970). Ceratoides lanata is a C_3 species whereas Atriplex confertifolia is a C_4 species (Welkie and Caldwell, 1970). Investigations into the productivity relationships of ecosystems containing these two species of contrasting photosynthetic pathway reveal few striking differences (Caldwell et al., 1977). In fact there was no reason to suggest that either species is at a competitive advantage in the salt-desert community (Caldwell et al., 1977). Yet long-term studies indicate that communities dominated by shadscale and winterfat are not compositionally stable (Stewart et al., 1940; Hutchings and Stewart, 1953; Holmgren and Hutchings, 1972; Norton, 1978). However, these studies were primarily directed at understanding the effect of livestock grazing on species composition and only Norton (1978) mentioned the possibility that changes in community composition unrelated to grazing were occurring.

One of the attributes which distinguish C_3 and C_4 plants is the degree to which they fractionate the stable carbon isotopes (^{12}C and ^{13}C) during photosynthesis. Both C_3 and C_4 photosynthetic types preferentially fix CO_2 containing ^{12}C ; C_4 plants, however, discriminate less against ^{13}C than do C_3 plants (Smith and Epstein, 1971; Bender, 1968, 1971; Troughton, 1971). The result of this fractionation of stable carbon isotopes during photosynthesis is a characteristic carbon isotope ratio (expressed as $\delta^{13}\text{C}$) in the plant tissue which serves as an effective marker for the occurrence of C_3 or C_4 photosynthesis. The $\delta^{13}\text{C}$ values of C_3 plants are between -23 and -34 ‰ whereas C_4 plants range from -9 to -19 ‰ (Smith and Epstein, 1971; Bender, 1968;

Troughton, 1971). There is an average difference of approximately 12-14 ‰ between mean C_3 and mean C_4 ratios (Bender, 1971; Troughton and Card, 1975; Troughton, 1972).

Many ecological questions are now being addressed utilizing carbon isotope analysis as the main tool of investigation. Such studies include seasonal biomass dynamics in mixed C_3/C_4 ecosystems (Ode and Tieszen, 1978; Boutton, pers. comm.; Tieszen et al., 1979a), herbivory and food chain analysis (Boutton et al., 1978; Fry et al., 1978a,b; DeNiro and Epstein, 1978a; Minson et al., 1975; Thayer et al., 1978; Tieszen et al., 1979b), and salt marsh ecosystem dynamics (Haines 1976, 1977). It is also likely that carbon isotope fractionation properties of plants will lead to a wide variety of paleoecological studies. This paper deals with an attempt to utilize carbon isotope ratios of soils to evaluate changes in C_3/C_4 dominance of salt-desert shrub communities.

The basis of such an investigation lies in the fact that the carbon isotope ratio of soil organic matter (and humic matter) is essentially derived from the plants and animals contributing to it. Theoretically, the $\delta^{13}C$ value of the soil organic matter should be identical to the existing vegetation at a site if 1) the vegetation has remained unchanged for a period of time equal to that of the oldest carbon in the soil profile, 2) the $\delta^{13}C$ value of atmospheric CO_2 has remained constant through time, 3) no fractionation of carbon isotopes has taken place in the soil as a result of decomposition processes, and 4) there is no differential preservation of plant compounds since different plant biochemical pathways can give rise to substances with markedly different $\delta^{13}C$ values compared to whole-plant values (Parker, 1964;

Degens et al., 1968; Park and Epstein, 1960; Smith and Benedict, 1974; Smith and Jacobsen, 1976; DeViro and Epstein, 1977). If assumptions 2 through 4 can be made and there is a difference in the $\delta^{13}\text{C}$ value between the soil and the vegetation then in all likelihood there has been some degree of compositional change in the C_3/C_4 biomass of the community.

The assumption that the $\delta^{13}\text{C}$ value of atmospheric CO_2 has remained constant over time is difficult to verify. It is known that the isotopic ratio of atmospheric CO_2 varies on a diurnal, seasonal and geographic basis. Keeling (1958, 1961) showed that the $\delta^{13}\text{C}$ value of air can vary by 3-4 o/oo on a daily basis in forest communities. Presumably as the CO_2 concentration in the forest is reduced by photosynthesis the ratio of $^{13}\text{C}/^{12}\text{C}$ increases as the result of the preferential utilization of ^{12}C by trees. The daily variation from more exposed habitats such as a beach or a mountain ridge was less than 1.0 o/oo (Keeling, 1958). In a comparison of $\delta^{13}\text{C}$ values of air sampled over a wide geographic area, Keeling (1961) found that the isotopic composition of CO_2 in the atmosphere varies only slightly (-6.7 to -7.4 o/oo). There also appears to be a seasonal variation of $\delta^{13}\text{C}$ values. Measurements taken over the Pacific Ocean near the coast of North America varied by only 0.5 o/oo over a one year period (Keeling, 1961). Similar evidence for a seasonal change is seen in the work of Lowdon and Dyck (1974). They demonstrated that the carbon isotope ratios of maple leaves became increasingly negative as the growing season progressed ranging from -22 o/oo to -28 o/oo. The fact that the isotopic ratio of the atmosphere may vary on daily and seasonal bases as well as geographically is not a serious

problem since the carbon isotope ratio of long-lived perennial plants is an average value reflecting average atmospheric conditions.

The assumption of stability in the carbon isotope ratio over long periods of time (millenium) is often made in spite of the fact that there is no direct evidence substantiating this claim. Evaluation of carbon isotopic variation in tree rings is complicated by the fact that fractionation of carbon isotopes by plants is temperature sensitive (Wilson and Grinstead, 1977; Troughton and Card, 1975; Smith et al., 1976). Generally, plants of the same species exhibit at most a 3-4 o/oo range of $\delta^{13}\text{C}$ values over a wide range of temperatures although Troughton and Card (1975) discovered that the agricultural species Triticum aestivum and Zea mays had more variable ratios. Smith et al. (1976) noted a trend for isotope fractionation to be least at the plant's optimal growth temperature and that the temperature dependence of the plants in their study was quite reproducible. Some caution is required in interpreting the results from studies where plants are grown in controlled environment chambers or greenhouses since the carbon isotope composition of such closed environments can be significantly different from that of the free atmosphere (Lerman, 1975). The majority of evidence supporting stability in atmospheric $\delta^{13}\text{C}$ over time is circumstantial. For example, isotopic ratios of coal derived from terrestrial sources are similar to those of modern day C_3 plants (Troughton, 1971). Similarly, the $\delta^{13}\text{C}$ value of a specimen of Atriplex confertifolia more than 40,000 years old (-13.4 o/oo) is close to present day values (-14.8 o/oo) (Troughton et al., 1974b).

There is some evidence that the $\delta^{13}\text{C}$ value of atmospheric CO_2 has changed recently. An analysis of isotopic variation in tree rings

of Bristlecone pine over the last 200 years, during which homogenous environmental conditions are assumed, revealed a decrease in the $\delta^{13}\text{C}$ value from -6.0 o/oo in 1850 to -6.9 o/oo at present (Wilson, 1978). This change to an isotopically lighter atmosphere (less ^{13}C) may have resulted from extensive clear-cutting of forests since such activity leads to the decomposition of tremendous amounts of organic material that is isotopically lighter than the atmosphere (Wilson, 1978). Stuiver (1978), using isotope data in conjunction with global carbon budgets, calculated that the atmosphere may currently be 1.4 o/oo lighter than it was in 1850. Half of the ^{13}C dilution is the result of fossil fuel combustion ($\delta^{13}\text{C} = -26.0$ o/oo) and the other half is due to agricultural related practices such as forest clearing (Stuiver, 1978). These changes are small in comparison to the differences between C_3 and C_4 plants.

Fractionation of carbon isotopes during soil decomposition has received little attention thus far and the available evidence is somewhat mixed. For example, $\delta^{13}\text{C}$ values of peats are either unchanged during decomposition (Troughton et al., 1974a) or become increasingly negative (isotopically lighter) with depth into the profile (Stout et al., 1975; Stout and Rafter, 1978). On the other hand, New Zealand mineral soils tend to have less negative values on the order of 2-3 o/oo with age indicating a slight fractionation during decomposition (Troughton et al., 1974a; Stout et al., 1975; Goh et al., 1977; Goh et al., 1976; O'Brien and Stout, 1978; Stout and Rafter, 1978). Part of this trend may be explained by the fact that the atmosphere appears to be about 1.0 o/oo isotopically lighter than it was 100 years ago (Wilson, 1978; Stuiver, 1978). Thus plants, which would tend to fractionate the same amount relative to the source through time, would

have had slightly less negative $\delta^{13}\text{C}$ values than they have now. This would be reflected in the soil organic matter as well. This alone is inadequate in explaining all the variation these workers have noted. Models aimed at determining whether a change of 3.0 o/oo in the $\delta^{13}\text{C}$ values of organic matter over a 100 cm depth (6500 year span) in a New Zealand pasture soil was due to microbial fractionation or a hypothetical change in vegetation were inconclusive in that both models predicted the distribution of $\delta^{13}\text{C}$ values with depth rather well (O'Brien and Stout, 1978). Still other studies indicate that no fractionation occurs during decomposition. Rafter and Stout (1970) found that the isotope ratios of fresh and four-year old beech leaves left in a nylon bag on the forest floor were similar. In another study the soil profile under a New Zealand conifer forest (Agathis australis) had a relatively uniform isotopic distribution with values of approximately -26 o/oo and -25 o/oo for fresh leaves and organic matter, respectively, at a depth of 100 cm (Stout et al., 1975). There seems to be a pattern of little soil fractionation in soils where decomposition is restricted such as peats and the Agathis forest, which are both characterized by the accumulation of undecomposed plant remains, and a slight enrichment in ^{13}C in mineral soils where plant debris does not accumulate (Troughton et al., 1974a; Stout and Rafter, 1978). The magnitude of this soil related fractionation should not be so large as to obscure gross changes in C_3 and C_4 vegetation types provided the change in vegetation has not occurred so long ago to have been obscured by the build-up of organic material from the current community.

Differential stability of plant biochemical fractions to degradation in the soil could also interfere with the technique since different

biochemical fractions such as starch, cellulose, lipids, etc. can have substantially different $\delta^{13}\text{C}$ values (Park and Epstein, 1960; Smith, 1975; Smith and Jacobsen, 1976; Smith and Benedict, 1974; DeNiro and Epstein, 1977). These studies show that most biochemical fractions differ in isotopic composition by only 1-3 o/oo from whole plant values. The major exception to this involves plant lipid material which is consistently isotopically lighter by 5-10 o/oo than whole-plant material (Park and Epstein, 1960; Smith and Epstein, 1971). Lipids have probably been the least studied of all soil organic compounds (Braids and Miller, 1975). Although some lipids can be rather resistant to decomposition for long periods of time (Oro et al., 1965), the majority of lipid material entering the soil decomposes within one year under aerobic conditions (Waksman et al., 1923; Waksman and Stevens, 1929; Springer and Lehner, 1952a,b; Lukoshko, 1965). In a study dealing with the fate of sterols in the soil, for example, Turfitt (1943) discovered that extreme acidity, poor aeration, and excess water content were important factors in the inhibition of sterol decomposition. In general, from the little work done on lipids in soils, differential preservation of isotopically lighter lipids from plants is unlikely in the majority of normal, well-drained soils.

In all then, there is little evidence suggesting that an evaluation of C_3/C_4 compositional changes in plant communities by analysis of the $\delta^{13}\text{C}$ values of soil organic matter is infeasible. The present study was initiated in an attempt to clear up discrepancies in interpretation of grazing impacts on salt-desert shrublands as well as to assess the status of community stability on a long-term basis. In accordance with these two objectives a brief review of grazing studies in salt-desert

communities and the biogeographic perspective of these communities is warranted.

The salt-desert ecosystem type has been a primary grazing area for sheep during the winter months since livestock grazing began in the mid-1800's. The result of heavy livestock utilization of the range during the winter and early spring has been a deterioration of the range. For example, Stewart et al. (1940) noted that the most palatable species including many grasses, Ceratoides lanata, Grayia spinosa and Artemisia nova exhibited a greater loss in density, higher mortality, greater decrease in reproduction and a larger decline in general vigor in the heavily grazed Wah Wah valley compared to the less heavily grazed Pine valley of western Utah. An analysis of the number of growth rings and the location of plants indicated that shadscale and winterfat coexisted in these communities when grazing began here and that shadscale was invading winterfat communities (Stewart et al., 1940).

In 1933, The Desert Experimental Range was established in southwestern Utah in order to gauge the effects of season and intensity of sheep grazing on salt-desert ranges. Unfortunately, the studies conducted and published over the years have employed a variety of pastures, plots and vegetation parameters which make direct comparisons among the studies difficult. The results of these studies are mixed and may in part reflect the different parameters measured.

Data on herbage yield trends for shadscale and winterfat communities covering a wide range of grazing treatments revealed that shadscale herbage yields increased under all grazing intensities during the 1935-1947 study period (Hutchings and Stewart, 1953). The increase was greatest at the lightest stocking rate. Winterfat herbage

yield in turn was greatest at the moderate stocking rate although its herbage yield also increased at all grazing intensities (Hutchings and Stewart, 1953). These same investigators also made the observation that *Atriplex* appeared to be more susceptible to drought than *Ceratoides*. Some twenty years later Holmgren and Hutchings analyzed the same plots in terms of changes in foliar plant cover as determined by the point-observation plot method (Stewart and Hutchings, 1936). This method approximated ground cover of an individual shrub when it had been compressed to eliminate gaps in the canopy. Thus it gives much lower percent cover values than would simple projection of the canopy outline. On pastures moderately grazed during the winter, the foliage plant cover increased for both shadscale and winterfat over the 32-year period (Holmgren and Hutchings, 1972). Winterfat cover decreased and that of shadscale increased, however, in pastures that were heavily grazed in late winter when some early spring growth has occurred (Holmgren and Hutchings, 1972). They concluded that shadscale was a more important element of cold-desert communities than it had been prior to exploitation of the range.

Another series of 9.3-m^2 rectangular plots had been established at the Desert Experimental Range in 1935. These plots were mapped periodically and contained plant cover of all perennial species (vertical projection of the canopy outline) as well as the location of all individual plants within the plots. In 1958 several of these plots were updated and the trends in species composition analyzed (Harper, 1959). The pastures used in this study included light, moderate and heavy early-winter grazing treatments as well as a heavy, late-winter treatment. Total plant cover increased on all the plots over the

23-year term but tended to increase more on the ungrazed control plots (Harper, 1959). Both shadscale and winterfat increased in percent cover during this time although, in terms of percent of total cover, shadscale had declined in importance whereas winterfat had increased in importance for all treatments except the heavily grazed, late-winter treatment (Harper, 1959).

In 1975 the heavily grazed plots from Harper's 1959 study were reviewed. The results indicate that winterfat populations have steadily declined in density while concomitantly increasing in percent cover since 1935 on both the grazed and ungrazed plots (Norton, 1978). Shadscale, on the other hand, exhibited increased density and percent cover up to 1958 on grazed plots and relatively unchanged density and percent cover on the control plots (Norton, 1978). Since 1958, however, shadscale density and percent cover values have plummeted considerably on both ungrazed and grazed plots (Norton, 1978). These trends in heavily grazed, shrubby pastures led Norton to conclude that grazing is not a major contributing factor to vegetation change in the salt-desert community.

It is obvious from this brief review that there is no consensus among investigators on just what is occurring at the Desert Experimental Range. That vegetation changes are occurring is evident but the exact nature of these changes is unresolved. Even though these studies represent one of the longest continuing grazing experiments ever conducted, the possibility exists that only minor fluctuations in plant populations that are relatively stable in the long-term view are being monitored. Alternatively, it is equally possible that these salt-desert communities are in the process of change and that a 45-year period is

simply not long enough to establish a definite trend in community change. Interpretation of vegetation change at the DER is clouded by the fact that plant growth is closely tied to precipitation regimes (Stewart and Hutchings, 1953) and that in some cases many years have elapsed between analysis of individual plots. This latter problem leads to a poor understanding of natural fluctuations in the populations of dominant salt-desert species. The specific role of drought and its effects on community stability are largely unknown. Furthermore, shadscale is relatively short-lived compared to winterfat (Harper, 1959; Norton, 1978; West, 1979) and the noise introduced into the system by the shorter turnover time of shadscale populations with respect to winterfat is unknown.

The exact origin of salt-desert communities is uncertain. Although currently a rather widespread community type, the persistence of this community throughout the Pleistocene is subject to speculation (Young et al., 1977; VanDevender and Spaulding, 1979). The main problem in assuming a chronologically coherent existence for this assemblage is that areas where salt-desert vegetation is best developed at present were under water during the pluvial phases of the Pleistocene (Eardley et al., 1957; Morrison, 1965; Mehringer, 1977). Little is understood about pluvial cycles before the Wisconsin glaciation, although the chronology for the last 30,000 years has been deciphered fairly well. Generally low lake levels from 40,000-25,000 years ago and deep lakes from 25,000-12,000 years ago seem substantiated (Morrison, 1965; Mehringer, 1977). Periods of low lake levels imply some combination of increased temperature/ decreased precipitation altering precipitation/ evaporation ratios such that the formation of permanent lakes does not

occur. Alternatively, high lake levels represent periods of lower temperature/higher precipitation compared to today resulting in P/E ratios conducive to the formation of permanent lakes (Antevs, 1952; Broecker and Orr, 1958; Snyder and Langbein, 1962). Since there are many possible combinations of precipitation and temperature giving the same P/E ratio exact values of the magnitude of such changes in the past are wanting.

As P/E ratios rose during the Pleistocene the basins dominated by Chenopod shrubland today were filled by lakes. Gross changes in the climate permitted some species from more mesic communities such as Pinyon-Juniper woodland and sub-alpine forest to migrate down mountainsides (Mehring, 1967). In all probability Pinyon-Juniper woodlands extended to the shores of the pluvial lakes since vertical migration of forest communities as great as 3,000-4,000 feet are indicated by pollen studies in the Las Vegas valley (Mehring, 1967). However, it is unlikely that the entire assemblage of species from a given community would respond similarly to these climate changes. Mixing of species from different plant communities did occur (VanDevender and Spaulding, 1979). The fate of the Chenopods during these cooler/moister pluvial phases is largely undocumented. Chenopods must have persisted somewhere as evidenced by the presence of Chenopod-Amaranth pollen in Pleistocene stratigraphic sequences (Mehring, 1967; Tidwell et al., 1972). Possibly these plants persisted around highly localized saline springs or retreated southward into the warm deserts. Recent analysis of packrat middens supports this latter notion (VanDevender and Spaulding, 1979). For example, fossil shadscale remains have been found in Sonoran and Mohave desert middens of late Wisconsin age,

although few other Great Basin species appear to have expanded south (VanDevender and Spaulding, 1979). Stutz (1973), in his analysis of *Atriplex* evolution, concludes that the explosive radiation of *Atriplex* in western North America has occurred since the end of the last pluvial some 10,000-12,000 years ago.

Most investigators of Great Basin chronology agree that by some 10,000-12,000 years ago the climate of the Intermountain West approached that of the present. Ancient Lake Bonneville had receded to within 30 m of its present level and has not surpassed that level since (Harper and Alder, 1970). By 8,000 years ago shadscale remains are known from cave deposits in northwestern Utah confirming the existence of salt-desert shrub communities here (Harper and Alder, 1970).

One has to be cautious in extrapolating climatic evidence from one area of the Great Basin to another, however, since climatic variation across the Great Basin can be sizable. The unevenness of tree ring growth is testament to this problem (Fritts, 1971). Therefore, in evaluating climatic fluctuations over the past 10,000 years, emphasis is given to studies closest to Curlew Valley in northwestern Utah, the site of the present study. Evidence considered includes archeological work at Hog-up cave (Harper and Alder, 1970); and pollen studies at nearby Crescent Springs (Mehring 1977), the Raft River Mountains (Mehring, 1977), and Swan Lake (Bright, 1966). Figure 1 presents a simplified summary of climatic fluctuations inferred by the authors of these studies. In general there is good agreement in the trends. The period from 12,000-8,000 years ago appears more mesic than

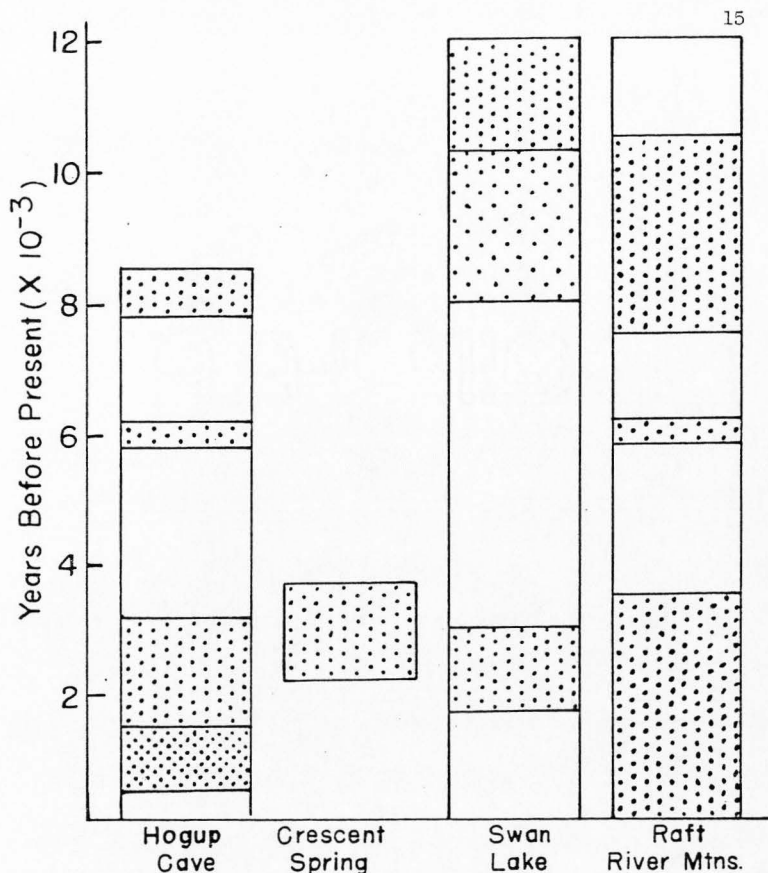


Figure 1. Summary of climatic variation in the northeastern Great Basin during the Holocene. Authors and interpretations are given in the text. Blank areas represent a climate similar to the present. Stippled areas represent periods of greater effective moisture. The density of stippling is proportional to the amount of effective moisture above present levels.

today and represents the final stage of the last pluvial. This is followed by a long (about 5,000 years) period of decreasing effective moisture with a brief increase around 6,000 years ago. This long, dry period roughly corresponds to the altithermal period of Antevs (1952). However, Antevs considers this time to represent conditions harsher than the present and this is not substantiated in these studies. Beginning approximately 3,200 years ago there is another increase in effective moisture followed by gradual drying out the the present climate. It appears that the climate of the northeastern Great Basin is as harsh as it has ever been over the past 12,000 years (Harper and Alder, 1970).

Since the climate has been relatively stable over the past 10,000 years and shadscale macrofossils appear in all levels at Hog up Cave (Harper and Alder, 1970), it seems safe to conclude that salt-desert communities have occupied the lowland valleys of northwestern Utah continuously over this period.

This study will focus on changes in the relative C_3/C_4 dominance that have occurred in the last several hundred years. Specifically, the hypothesis that shadscale (C_4) importance is increasing in salt-desert communities will be tested.

The time frame of this study is dictated by the age of the soil carbon which in turn is governed by decomposition processes. These desert soils are characterized by extremely low carbon content, usually less than 1%. Inherently low plant productivity and rapid decomposition rates, which occur when conditions are favorable (West and Skujins, 1978), are responsible for the low organic carbon levels. Kononova (1966)

has noted a similar relationship between low organic carbon and high decomposition rates in Serozem soils of the USSR. The rapid decomposition rates probably result in a comparatively short turnover, or mean residence time, for organic carbon of less than 500 years.

Radiocarbon dating of the soils would certainly offer some time perspective but such dates can greatly underestimate the age of soils if an appreciable amount of nuclear-bomb-produced ^{14}C is present in the organic matter (Campbell et al., 1967). The degree of enrichment by bomb-produced ^{14}C will depend on plant productivity, rooting patterns and soil mixing by invertebrates. Low plant productivity leads to a smaller amount of ^{14}C entering the community through photosynthesis. On the other hand the extensive root distribution of Chenopod shrubs will tend to distribute the ^{14}C throughout the soil profile. The effect of different rooting patterns on radiocarbon enrichment of soils can be seen in a comparison of forest and grassland vegetation. Subsoils under the deep-rooted forest vegetation exhibit considerably more ^{14}C -enrichment than subsoils under the shallow-rooted grassland vegetation (Stout and O'Brien, 1972). The low productivity of most salt-desert shrub communities minimizes ^{14}C incorporation but the extensive rooting pattern probably distributes the assimilated ^{14}C evenly in the profile. As such the usefulness of ^{14}C -dating cannot be determined in advance for these soils.

Two alternative approaches to relative age stratification are used in this study. First, each particular sampling core is subsampled at various depths since, in general, there is a good correlation between soil age and soil depth (Goh et al., 1976; Jenkinson, 1975; Jenkinson

and Rayner, 1977). Secondly, some samples have been fractionated into humin, humic acid and fulvic acid by conventional techniques. Such organic fractions can show significant differences in age or mean residence time (Jenkinson, 1968; Persson, 1968; Goh et al., 1977; Campbell et al., 1967). Other studies have demonstrated significant differences in the stable carbon isotope ratios of these organic fractions (Nissenbaum and Schallinger, 1974; Campbell et al., 1967).

Although the results of this study do not provide unequivocal assessment, the data at this time appear to support the hypothesis that shadscale is encroaching into areas previously dominated by winterfat.

METHODS

Study area

The study site is located in Curlew Valley, Utah ($41^{\circ}52' \text{ N}$, $113^{\circ}5' \text{ W}$) at an elevation of 1350 m. This broad, lacustrine valley extends northward from the northernmost extent of the Great Salt Lake and was largely inundated by the waters of Lake Bonneville during the last pluvial of the Pleistocene era. Valley soils are generally homogenous and vary in texture from silt-loam to sandy-loam. Soil profiles are of the Thiokol series, a fine silty mixed mesic family of xerollic calciorthids (Skujins and West, 1973). The soils are highly calcerous in nature with carbonates comprising 10-25% of the soil by weight.

This site was chosen because it represented typical salt-desert shrubland with Atriplex confertifolia and Ceratoides lanata as dominants. In addition, there exists a large data base on the soils and vegetation of the area (Gates et al., 1956; Mitchell et al., 1966; Gasto, 1969; Caldwell et al., 1977; Holthausen, 1977). Both of the dominant shrubs commonly occur in nearly monospecific stands at the site and as such present an ideal opportunity for soil carbon isotope study. The climate of the area is typical of that found throughout lowland valleys of the Intermountain West and has been summarized elsewhere (Caldwell et al., 1977).

Curlew Valley has been grazed, principally by sheep, for about 100 years. It is currently grazed by both sheep and cattle. The actual study site, however, is located within an enclosure and has not been grazed during the past ten years (Rice and Westoby, 1978). Prior to that the site area was used as a lambing grounds. For a detailed review of the grazing history of the area see Rice and Westoby (1978).

Transects

Preliminary cores taken in 1976 revealed that significant differences existed between the carbon isotope ratios of soil organic matter and the current community vegetation. In the summer of 1977 three transects were laid out in areas where the ecotone between adjacent stands of shadscale and winterfat was abrupt and where disturbance, as indicated by the presence of two weedy annuals, Bromus tectorum and Halogeton glomeratus, was minimal. The transects were 25-35 m in length and stretched from well within the 'pure' winterfat stand, across the ecotone and into the 'pure' shadscale stand. Location of the transects and other sampling points in relation to vegetation is shown in Figure 2. Vegetation along the transects was characterized by the line-intercept estimate of plant cover which provided a quantitative measure of how shrub dominance varied along the transects.

The soil and litter layer were sampled at both ends of the transect and at regular intervals along the transect. After removal and bagging of the litter, the soil was sampled with a 8.5 cm diameter soil auger to a depth of 45 cm. The cores were subdivided into three 15-cm segments representing the 0-15 cm, 15-30 cm and 30-45 cm soil depths. Three other cores, whose location is indicated in Figure 2, were sampled as above except to 100 cm depth. In all, 18 cores representing 62 samples were taken. Soil and litter samples were transported back to the lab and oven dried at 105 C.

Sample Preparation

Over-dry soil and litter samples were shaken on a series of sieves of decreasing diameter to remove roots and other visible debris. Larger

plant fragments (largely roots) were manually removed from the sieves and smaller fragments were removed by flotation in ZnCl_2 solution (density = 1.8). Separated plant fragments were washed successively with .1 N HCl and distilled water then collected by filtration. This undecomposed organic matter, which was largely roots, and the litter samples were oven dried at 70 C and ground into a fine powder with a pica-mill blender (Pitchford Industries) for mass spectrometry analysis.

Soil passing through the smallest sieve (diameter = .127 mm) was collected and wet extracted in saturated NaCl solutions (Fernandez and Caldwell, 1975) until no debris was found floating on the surface. The soil was then washed several times to remove excess salt and oven dried at 70 C. Microscopic examination of soils at this point revealed that the samples were clear of any undecomposed material.

A 50-g subsample of root-free soil was acid-washed in dilute (.1-.5 N) HCl to remove carbonates. Because of the high percentage of carbonates in these soils decalcification was not considered complete until the soil solution pH stabilized for 24 hr. Decalcified soils were subsequently washed three times in distilled water, centrifuged and oven dried at 105 C. A small subsample (.3-.5 g) of decalcified, root-free soil was used for mass spectrometric determination.

Humate Fractionation

Approximately 40 g of previously decalcified, root-free soil was intermittently shaken for 24 hr under nitrogen in 200 ml of .5 N NaOH. The supernatant was decanted and saved while the residue was again extracted in 200 ml of .5 N NaOH, this time for 1 hr. The supernatant was collected after centrifugation and the residue washed in distilled water. Following centrifugation the supernatant was collected and pooled

with the other two supernatants. The residue was oven-dried at 70 C and represented the 'humin' fraction. The supernatant was adjusted to pH 1 with concentrated HCl followed by centrifugation at 10,000 g. The supernatant was decanted and dialyzed against distilled water in dialysis tubing (Spectrapor Co.) (MWCO = 2000) for seven days and then oven-dried at 70 C. This represented the 'fulvic acid' fraction of soil humic material. The acid precipitate was purified by redissolving in NaOH and reprecipitating with HCl followed by centrifugation. This purification procedure was repeated and the precipitate was oven-dried at 70 C to give the 'humic acid' fraction of soil humic material.

Mass Spectrometry

Carbon isotope determinations were performed in the laboratory of Bruce N. Smith at Brigham Young University according to the procedures outlined by Smith (1976). Results are expressed in standard $\delta^{13}\text{C}$ notation where

$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

and R = mass 45/ mass 44 of sample or standard CO_2 . Standard CO_2 is carbonate CO_2 from the fossil skeleton of Belemnitella americana from the Pee Dee formation of South Carolina (PDB).

RESULTS

The abruptness of the ecotone between neighboring stands of winterfat and shadscale is clearly depicted in the photographs of the three transects used in the study (Figure 2). The location of these transects in relation to the dominant vegetation is shown in Figure 3. The change from complete C_3 shrub cover to complete C_4 shrub cover occurs over a distance of about 20 m along the transects.

This change in dominance is reflected in the increasing (less negative) $\delta^{13}C$ value of root and litter carbon as one approaches the shadscale stand (soil cores are numbered starting in the winterfat community). For example, core-1 on transect 1 (winterfat dominance) has a litter $\delta^{13}C$ value of -23.5 o/oo and a root $\delta^{13}C$ value of -24.6 o/oo (Table 1) which is comparable to the -25.3 o/oo value for winterfat alone. Any significant deviation above this expected value of -25.3 o/oo would indicate the presence of carbon derived from the C_4 shadscale which has a $\delta^{13}C$ value of -13.0 o/oo. The influence of shadscale on the litter and root carbon components of the community is evident in core-6 on transect 1 (Table 1). Litter and roots have a $\delta^{13}C$ value of -21.2 o/oo and -19.7 o/oo, respectively. A $\delta^{13}C$ value of approximately -19.0 o/oo in a sample would indicate an equal amount of carbon derived from C_3 and C_4 plants.

In this study there are three separate measurements of relative C_3/C_4 dominance along each transect. The line-intercept estimate of plant cover reflects changes in aboveground shrub dominance. The carbon isotope ratio of surface litter also mirrors C_3/C_4 shrub distribution but quantifies the proportion of C_3/C_4 carbon entering the soil from the surface. Finally, the $\delta^{13}C$ value of roots provides an estimation



Transect #1



Transect #2



Transect #3

Figure 3. Photographs of the three transects analyzed in the study.

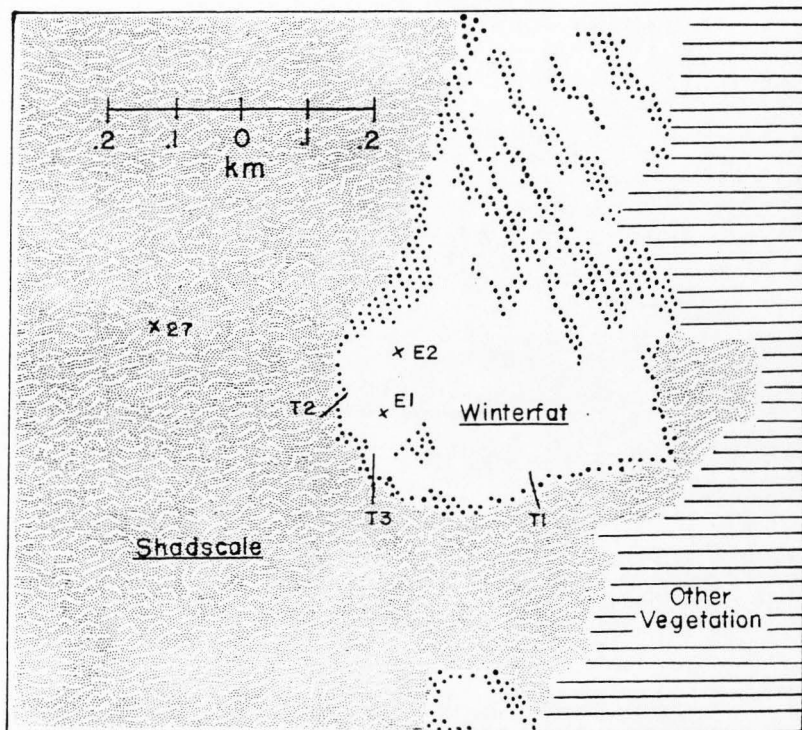


Figure 3. Map of the dominant vegetation and sample location at the study site in Curlew Valley, Utah. Areas where both winterfat and shadscale occur are indicated by stippling. Map coordinates are R.2 W, T.12 N, section 15, Salt Lake City meridian.

Table 1. $\delta^{13}\text{C}$ values of litter, roots and soils from transect #1.
 Sample combustions and isotope determinations have a combined
 standard deviation of 0.1 o/oo. Vegetation cover key is:
 W=winterfat, S=shadscale and W/S=mixed winterfat/shadscale.

Core #	Vegetation Cover	Depth (cm)	$\delta^{13}\text{C}$ -litter	$\delta^{13}\text{C}$ -roots	$\delta^{13}\text{C}$ -soils
1	W	surface	-23.5		
		0-15		-24.6	-21.0
		15-30		-24.4	-20.5
		30-45		-24.0	-20.5
2	W	surface	-23.6		
		0-15		-23.7	-22.0
		15-30		-24.2	-21.1
		30-45		-23.7	-21.1
3	W	surface	-24.1		
		0-15		-22.8	-21.3
		15-30		-24.6	-21.2
		30-45		-24.4	-21.1
4	W/S	surface	-24.0		
		0-15		-23.6	-21.3
		15-30		-24.4	-21.2
		30-45		-22.3	-20.8
5	W/S	surface	-19.8		
		0-15		-24.3	-20.8
		15-30		-23.9	-20.8
		30-45		-23.4	-20.7
6	S	surface	-21.2		
		0-15		-19.7	-20.1
		15-30		-20.2	-20.3
		30-45		-22.3	-20.4
7	S	surface			
		0-15		-20.8	-20.7
		15-30		-20.3	-20.2
		30-45		-20.7	-19.5
		45-60		-21.3	-19.8

of belowground C_3/C_4 biomass. This is an important measurement because although the soil volume in the upper 50 cm of the profile is thoroughly explored by roots in this community (Caldwell et al., 1977), the lateral distribution of roots from individual shrubs is unknown.

Variation in the $\delta^{13}C$ value of soils is quite small in relation to both depth in the profile and location on a transect (Table 1). Thus, root and soil isotope ratios were averaged for each core and the means graphically summarized in Figures 4,5, and 6. Changes in shrub dominance and litter $\delta^{13}C$ values are presented in the upper portion of each graph. The $\delta^{13}C$ values of all samples from transects #2 and #3 are given in Appendix A and Appendix B, respectively. Shadscale and winterfat accounted for 84%, 98% and 98% of all cover on transects 1,2 and 3, respectively. Actual ground cover was 34%, 39% and 38% on transects 1, 2 and 3, respectively.

The $\delta^{13}C$ value of litter and roots on transect 1 become less negative as the percent of C_4 cover increases from 0% to 100%. The increase in the $^{13}C/^{12}C$ ratio is insufficient to support the notion that there has been persistent 100% dominance by C_4 plants as the cover data indicates. This discrepancy is not surprising since the line-intercept measure of ground cover does not incorporate the variability in plant cover around a specific sampling point. Both winterfat and shadscale stands include numerous individuals of the C_3 grasses Bromus tectorum and Sitanion hystrix which undoubtedly contribute to the carbon pools of the community. The $\delta^{13}C$ values of soil organic carbon, however, are relatively uniform along transect 1 despite the sudden shift from C_3 cover to C_4 cover. The total variation of $\delta^{13}C$ values

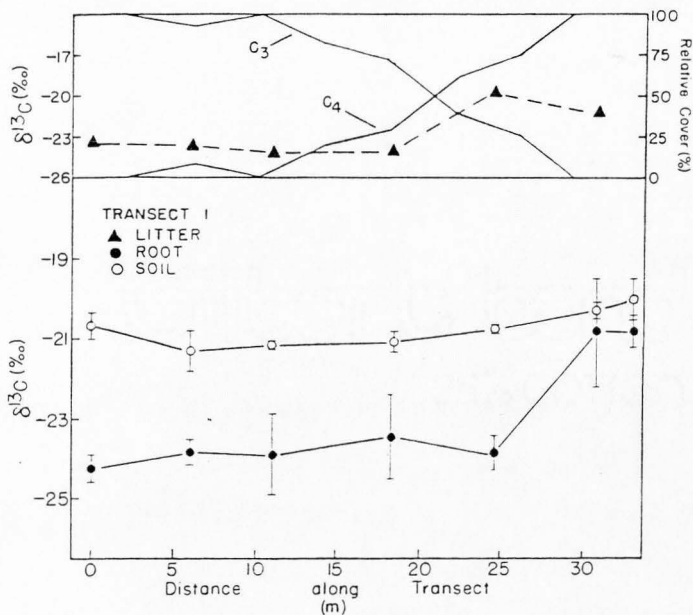


Figure 4. Carbon isotope ratios of litter (▲), roots (●) and soils (○) in relation to relative C₃/C₄ cover along transect #1. Soil and root values are the mean of at least three determinations. Error bars represent ± one standard deviation.

(Table 1) is 2.0 o/oo. The range for core means (average of three depths) is 1.2 o/oo (Figure 4). Values are slightly higher (-20.2 o/oo) in soils under shadscale than in soils under winterfat (-21.0 o/oo). The organic carbon along transect 1 is comprised of roughly 65% carbon derived from C_3 plants assuming a $\delta^{13}C$ value of -25.0 o/oo and -13.0 o/oo for 'pure' C_3 - and C_4 -derived carbon, respectively. Such calculations are made with the assumptions that the plant material is not further fractionated by the processes of decomposition and the productivity relationships of the dominant shrubs are comparable, as will be discussed in greater detail later.

The $\delta^{13}C$ values of roots and soils are parallel along this transect until shadscale assumes dominance. The soil-root difference averages 2.9 o/oo over the first five cores. The lack of a consistent difference between root and soil $\delta^{13}C$ values indicates that a shift in vegetation has likely occurred, regardless of whether fractionation during humification is present. To clarify this point, assume for the moment that the observed 2.9 o/oo difference is due to fractionation in the soil, i.e., that as fresh plant material is transformed into stable humic matter there is a preferential loss of the lighter ^{12}C isotope due to the metabolic activities of soil organisms. The remaining stable organic matter is then enriched in ^{13}C resulting in a higher $\delta^{13}C$ value compared to the plant material from which it originated. Such fractionation would affect all carbon entering the soil and be of equivalent magnitude for carbon derived from all plant species. Thus a shadscale community with root and soil isotope ratios similar to core-6 should have a soil carbon $\delta^{13}C$ value closer to -18.0 o/oo if it has dominated this area sufficiently long. Thus, if the ecotone between

shadscale and winterfat stands has been relatively unchanged for several hundred years, the trend lines for root and soil $^{13}\text{C}/^{12}\text{C}$ ratios should be parallel at all points. Since they are not parallel this may indicate that shadscale has only recently assumed dominance in this area.

On the other hand, in the absence of fractionation during decomposition soil and root $\delta^{13}\text{C}$ values should be equal. This is the case with roots and soils under shadscale at the present time (cores 6 and 7). The 2.9 o/oo difference under winterfat would indicate increasing dominance by this C_3 species. The relative merits of each of these interpretations will be discussed in depth later.

The trends for percent C_4 cover and litter, root and soil $\delta^{13}\text{C}$ values for transect 2 are similar in most respects to transect 1 (Figure 5). Mean soil $\delta^{13}\text{C}$ values (average of three depths) vary from -21.5 o/oo at core-1 to -20.7 o/oo at core-4. However, there is no marked change in the soil-root relationship as in transect 1. However, a slight trend toward smaller root-soil differences under shadscale does exist. The low $\delta^{13}\text{C}$ value of -23.0 o/oo for roots at core-5 where plant cover and litter $\delta^{13}\text{C}$ data suggest dominance by C_4 plants is difficult to understand. The persistence of roots from a weedy C_3 annual such as Bromus tectorum could contribute to this low isotopic ratio. As on transect 1, $\delta^{13}\text{C}$ values of soils are higher under C_4 vegetation than under C_3 vegetation.

The data from transect 3 (Figure 6) mirrors that from transect 1 except that root and soil $\delta^{13}\text{C}$ values are not as uniform. The 2.4 o/oo spread of $\delta^{13}\text{C}$ values is greater than in transects 1 and 2 but the same

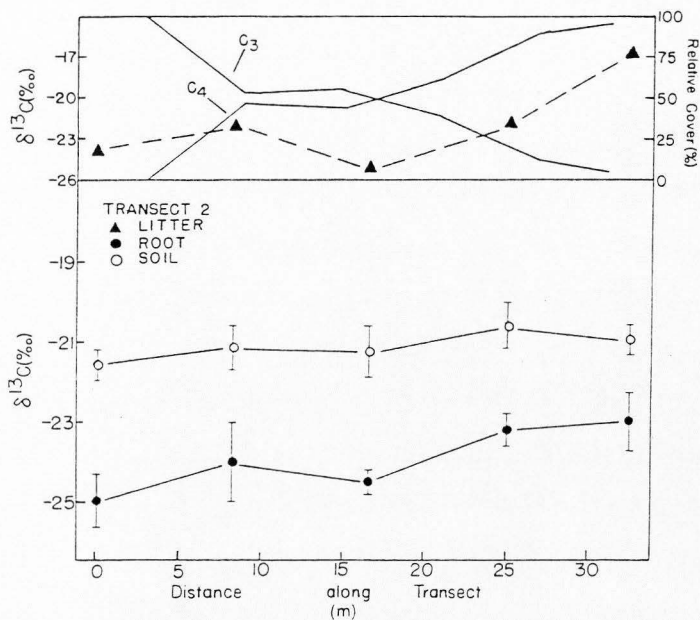


Figure 5. Carbon isotope ratios of litter (▲), roots (●) and soils (○) in relation to relative C_3/C_4 cover along transect # 2. Soil and root values are the mean of at least three determinations. Error bars represent \pm one standard deviation.

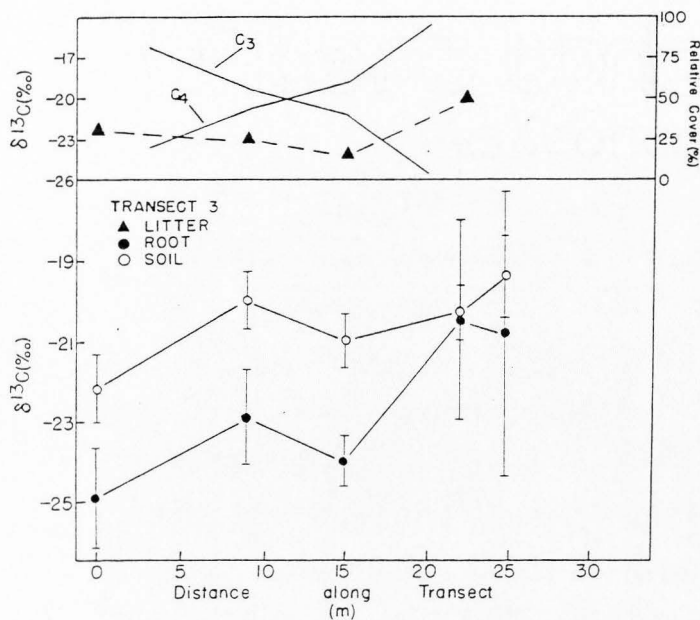


Figure 6. Carbon isotope ratios of litter (▲), roots (●) and soils (○) in relation to relative C₃/C₄ cover along transect # 3. Soil and root values are the mean of at least three determinations. Error bars represent ± one standard deviation.



Figure 7. Photograph of a winterfat-dominated area from transect #3.
A dead shadscale is behind the stake.

trend toward higher $^{13}\text{C}/^{12}\text{C}$ ratios under shadscale exists. Interestingly, the highest average soil $\delta^{13}\text{C}$ value is found in core-2 where winterfat dominates. The most plausible explanation for this phenomenon can be found by examining the photograph of this core (Figure 7). The core is surrounded by winterfat plants with the exception of a single, dead shadscale individual (immediately behind the stake). Apparently this individual lived long enough to contribute significantly to the organic carbon pool in the soil but has been dead sufficiently long that it no longer contributes to the litter or root carbon pools at this location. Soil $\delta^{13}\text{C}$ values average 2.8 o/oo higher than root $\delta^{13}\text{C}$ values over the first three cores but are nearly equal for the shadscale cores. Transect 3 resembles transect 1 in that respect and the general interpretations that have been previously given for these trends apply.

In addition to the 17 cores from the transects three supplementary cores, the location of which is shown in Figure 3, were analyzed. Cores E1 and E2 represent extensions of the transects 50 m and 100 m further into the winterfat stand. Core 27 was located about 500 m west of the transects in a region where dominance by C_4 vegetation is best developed. The results from these cores are given in Table 2.

Cores E1 and E2 are similar to transect cores under winterfat to a depth of 45 cm. The samples from 45-100 cm in the profile have higher $\delta^{13}\text{C}$ values, however, than the samples nearer to the surface. The $\delta^{13}\text{C}$ values of the two 75-100 cm samples are 3.3 o/oo and 2.1 o/oo higher than the 0-15 cm samples in the same cores.

Core 27, as examination of root $\delta^{13}\text{C}$ values indicates, is located in an area of complete dominance by C_4 vegetation. As a result soil

Table 2. $\delta^{13}\text{C}$ values of roots and soils from the supplementary cores. Sample combustion and isotope determinations have a combined standard deviation of 0.1 o/oo. Vegetation cover key is: W= winterfat and S=shadscale.

Core #	Vegetation Cover	Depth (cm)	$\delta^{13}\text{C}$ -roots	$\delta^{13}\text{C}$ -soils
E1	W	0-15	-24.8	-22.5
		15-30	-25.5	-21.7
		30-45	-26.1	-21.6
		45-75	-26.0	-20.3
		75-100		-19.2
E2	W	0-15	-24.9	-21.5
		15-30	-25.0	-20.6
		30-45	-26.2	-21.1
		45-60	-23.7	-20.5
		60-75	-22.7	-19.7
		75-100	-25.9	-19.4
27	S	0-15	-11.7	-16.6
		15-30	-11.5	-16.6
		30-45	-11.5	-16.1
		45-60	-11.6	-18.5
		60-75	-12.3	-17.9
		75-100	-11.1	-18.5

$^{13}\text{C}/^{12}\text{C}$ ratios are higher here than at any other sampling location. The average soil $\delta^{13}\text{C}$ value for this core is -17.4 o/oo and suggests that on the order of 65% of the soil carbon is derived from C_4 sources. The trend for the samples at 45-100 cm depth is opposite that from cores E1 and E2. The $\delta^{13}\text{C}$ values become more negative with depth here. It is possible that these trends offer important clues to the vegetation history of the area, but the lack of extensive samples at these depths precludes interpretation at this time.

The results of soil fractionation of six samples is given in Table 3. The samples analyzed were from the number one cores of transects 2 and 3. Substantial differences exist among these fractions. In all cases fulvic acid yields the highest $\delta^{13}\text{C}$ value, humin is intermediate, and humic acid is lowest. Since 80-90% of the soil organic carbon remained in the humin fraction following extraction, its isotope ratio was quite similar to that for total soil organic carbon. An interpretation of these potentially significant differences cannot be formulated without knowledge of the relative ages of the fractions. If the fractions segregated out chronologically they could perhaps offer the best approach to understanding the vegetation history of this site. The problems of interpretation of these soil organic matter fraction have been pointed out elsewhere (Stout and Rafter, 1978) and will be elaborated on later.

Table 3. $\delta^{13}\text{C}$ values of soil organic matter fractions. Both cores are from areas of winterfat dominance. Bulk soil represents soil prior to fractionation.

Transect #	Core #	Depth (cm)	$\delta^{13}\text{C}$ -bulk soil	$\delta^{13}\text{C}$ -humin	$\delta^{13}\text{C}$ -humic acid	$\delta^{13}\text{C}$ -fulvic acid
2	1	0-15	-22.0	-21.6	-24.1	-21.0
		15-30	-21.6	-21.7	-22.3	-20.0
		30-45	-21.3	-21.2	-23.6	-19.5
3	1	0-15	-23.1	-23.4	-24.4	-23.3
		15-30	-22.1	-22.1	-23.8	-21.2
		30-45	-21.4	-21.7	-24.1	-19.9

DISCUSSION

In this study $\delta^{13}\text{C}$ values of soil organic carbon are used as a measure of past C_3/C_4 dominance in the salt-desert community. But the $\delta^{13}\text{C}$ value does not reflect dominance in the physical sense of occupation of space or soil volume; rather, it reflects dominance in the more dynamic sense of productivity. That is, the $\delta^{13}\text{C}$ value is an estimate of the relative C_3/C_4 productivity integrated over a long time period at a particular location. This is an important distinction because relative long-term productivity cannot be directly compared with static community parameters such as relative percent cover, relative biomass, or even $\delta^{13}\text{C}$ value of roots, unless the productivity of the species under consideration are comparable.

For example, assume that two species of contrasting photosynthetic pathway are growing side by side and both species have identical belowground biomass, but the C_4 species has twice the annual root turnover of the C_3 species. Assuming a $\delta^{13}\text{C}$ value of -25 o/oo and -13 o/oo for the C_3 and C_4 species, respectively, a $\delta^{13}\text{C}$ value of -19 o/oo would be expected for roots in a soil volume equally occupied by the two species. But the soil organic matter in such a situation would probably be closer to -16 o/oo since nearly two-thirds of the carbon that enters the soil via root turnover each year is from the C_4 species. In such a situation the $\delta^{13}\text{C}$ value of roots does not accurately reflect the annual root productivity and the importance of the C_3 species in the community is overestimated on a productivity basis. Fortunately, the annual productivity components of shadscale and winterfat are similar in most respects (Caldwell et al., 1977) and root and litter $\delta^{13}\text{C}$ values should be a reliable index of relative

C_3/C_4 productivity.

Precise interpretation of carbon isotope ratios of soil organic matter is also dependent on a proper understanding of the organic carbon cycle. For example, unless the species contributing to soil organic matter behave similarly during decomposition; that is, unless their decomposition rates and turnover times are similar, the $\delta^{13}C$ value of soil organic matter could be biased. If shadscale herbage was generally more resistant to decomposition in the soil than winterfat herbage, the $\delta^{13}C$ value of soil organic matter would tend to overestimate long-term relative C_4 productivity even if annual productivity rates are similar. Because of the lack of information on decomposition processes in this community, the potential significance of this problem cannot be assessed. There is reason to be cautious about this since the relative decomposition rates of grass roots is dependent on C:N ratios, lignin content and carbohydrate content (Herman et al., 1977).

Probably the most important confounding factor involved in the use of stable carbon isotope ratios to assess community vegetation changes is fractionation of isotopes in the soil. Does it exist in all soils, and to what degree? Such fractionation can occur in two ways. Differential preservation of plant compounds with significantly different isotopic ratios than the whole plant could lead to fractionation as could direct biochemical fractionation of ^{12}C and ^{13}C during microbial assimilation and respiration.

As pointed out previously, small isotopic differences exist among various plant compounds (Park and Epstein, 1961; Parker, 1964). With the exception of lipids these isotopic variations are small. However, since lignins in plants are particularly resistant to degradation in the soil

(Kononova, 1966), even small isotopic differences could lead to a systematic deviation from expected soil $\delta^{13}\text{C}$ values. Unfortunately, little information on carbon isotope variation in lignins is available. Park and Epstein (1961) showed that the $\delta^{13}\text{C}$ value of lignin from tomato was 1.0 o/oo less negative than the $\delta^{13}\text{C}$ of the entire plant. Wilson and Grinstead (1977) uncovered a consistent difference of 3.0 o/oo between lignin and cellulose extracted from the same annual growth rings of Pinus radiata. Whether such isotopic differences are common among woody plants and whether lignin tends to be isotopically lighter or heavier than the plant as a whole is unknown.

A second possible pathway of fractionation in the soil is that due to microbial assimilation and respiration. Although isotopes of the same element have electronic, translation and rotation energies that are equal, there are small differences in the molecular vibrations of isotopes (Hoefs, 1973). As a consequence, chemical bonds formed by the lighter isotope of an element are more readily broken than bonds formed by the heavier isotope (Hoefs, 1973). As soil microorganisms degrade plant material and synthesize new molecules there could be a tendency for molecules containing ^{12}C to react and be respired more readily than molecules containing ^{13}C . Thus one might expect that the humified organic matter would be enriched in ^{13}C relative to the completely decomposed organic matter. The degree of such fractionation, if any, has not been determined. Experiments comparing the $\delta^{13}\text{C}$ values of animals and their diets show that animals have $\delta^{13}\text{C}$ values that average 1.0 o/oo less negative than the $\delta^{13}\text{C}$ value of their diets (DeNiro and Epstein, 1978b). This implies that a slight fractionation of stable carbon isotopes with respect to the food source has occurred. Park and

Epstein (1961) followed the $\delta^{13}\text{C}$ value of respired CO_2 from tomato plants over time. Toward the end of the experiment, when bacterial decay set in, the $\delta^{13}\text{C}$ value of respired CO_2 became increasingly negative. They attributed this to a combination of preferential decomposition of lipids and fractionation during microbial respiration (Park and Epstein, 1961). Thus, there is some evidence supporting a slight fractionation of carbon isotopes during assimilation and respiration processes in general and it would appear likely to occur in soils as well. The magnitude of such fractionation, however, would not appear to be more than a few per mil.

This agrees with field observations of soil and vegetation $\delta^{13}\text{C}$ values in well drained mineral soils (Troughton et al., 1974a; Stout et al., 1975; O'Brien and Stout, 1978; Stout and Rafter, 1978). However, these studies make the critical assumption that the vegetation of a particular site has remained unchanged during the period of carbon accumulation in the soil. In addition, these observations were made on soils under vegetation from more mesic environments than the present study and the relevance of this particular pattern to arid soils may be questionable.

The overall evidence points to soil fractionation as being a small but significant factor in interpretation of soil organic matter-vegetation relationships, and the data in the present study also appear to indicate that fractionation of stable carbon isotopes in the soil occurs. The $\delta^{13}\text{C}$ values of roots and soils differed by a nearly constant magnitude in areas under winterfat dominance (Figures 4, 5 and 6). This uniform differential of about 3.0 o/oo was found 100 m away from the transects in cores E1 and E2. Such uniformity of soil carbon

isotope ratios would suggest long-term stability in the soil organic cycle. This vegetation-soil difference vanishes in samples from the shadscale side of the ecotone (Figures 4, 5 and 6). This change is caused by a progressive increase in the $\delta^{13}\text{C}$ value of roots as shadscale becomes dominant along the transects, although the $\delta^{13}\text{C}$ value of soil also increases slightly. Soils under shadscale do not exhibit a uniform soil-root $\delta^{13}\text{C}$ differential as do soils under winterfat. For example, in core-27 (Table 2) the $\delta^{13}\text{C}$ values of roots are always less negative than the $\delta^{13}\text{C}$ values of soils. A similar pattern is found in transect 3 samples from core-4 and core-5 (Appendix B). These trends indicate a very recent arrival of shadscale, since it is unlikely that fractionation of stable carbon isotopes would ever lead to a soil that is isotopically lighter than the vegetation, at least in well-drained soils. In all the cores from winterfat-dominated areas the $\delta^{13}\text{C}$ value of soils is consistently higher than the $\delta^{13}\text{C}$ value of the vegetation. This indicates that soil fractionation leads to a soil carbon that is 3.0 ‰ heavier than the vegetation. As such, the data suggest that an increase in shadscale is underway in this community. In drawing this conclusion the assumption is made that the contribution of carbon from other species in the plant community has been insignificant compared to the contribution of winterfat and shadscale.

An alternative interpretation could suggest that winterfat rather than shadscale is increasing. This interpretation would be based on the assumption that soil age increases with soil profile depth as is assumed for most soils (Goh et al., 1977; Jenkinson, 1975; Jenkinson and Rayner, 1977). This assumption is based to a large degree on the rate of diffusion of organic carbon into the soil profile (O'Brien and

Stout, 1978). This is particularly true in many ecosystems where the bulk of the carbon enters the soil at the surface and gradually diffuses downward. Organic carbon at greater depths is older simply because the diffusion path from the surface is longer. Following this reasoning, one would expect that the carbon in the 30-45 cm samples would represent older carbon than that in the surface samples. In nearly every core there is a trend for the $\delta^{13}\text{C}$ value of soil carbon to be less negative with depth although the magnitude of change is small (Tables 1 and 2). This trend would suggest that the allegedly older carbon has a greater proportion of carbon derived from C_4 plants than does the younger carbon closer to the surface. Therefore, increasing winterfat dominance explains this pattern. But this analysis of $\delta^{13}\text{C}$ distribution with depth is not so straightforward in salt-desert shrub communities. The extensive and diffuse rooting systems of these shrubs coupled with the unusually high root/shoot ratios (Fernandez and Caldwell, 1975) indicate that the majority of plant biomass in this community is belowground. Even when one considers the proportion of above- and belowground turnover it is obvious that most carbon does not enter the soil at the surface in this community (Caldwell et al., 1977). As a result, the distribution of carbon is likely to be governed more by root distribution than by soil diffusion characteristics. In addition, one would expect that diffusion of organic carbon through the soil profile is limited since these soils are extremely dry throughout most of the year. Thus, even though the distribution of $\delta^{13}\text{C}$ values with depth may be a useful approach in some ecosystems, its usefulness in this ecosystem is very questionable.

Unfortunately, the isotopic ratios of soil organic matter

fractions in this study are not easily interpreted. Previous studies involving radiocarbon dating of 'humic acids' and 'fulvic acids' indicate that in general 'fulvic acids' are younger than 'humic acids' (Jenkinson, 1975; Campbell et al., 1967; Paul et al., 1964), although Goh et al. (1977) concluded that 'humic acids' were younger because they contained more 'bomb' ^{14}C than did 'fulvic acids'. The six chemically fractionated soils analyzed in this study were from areas of complete winterfat dominance (Table 3). If 'fulvic acid' is younger than 'humic acid' one would expect the $\delta^{13}\text{C}$ value of 'fulvic acid' to be comparable to the $\delta^{13}\text{C}$ value of winterfat, i.e. -25.0 o/oo. However, it is the 'humic acid' fraction that most resembles winterfat carbon isotope ratios (Table 3). This suggests that 'humic acid' is younger than 'fulvic acid'. 'Fulvic acid' $\delta^{13}\text{C}$ values are less negative. This may be the result of a greater contribution of carbon from C_4 vegetation to this fraction. If the 'humic acid' fraction represents the youngest soil fraction, it would indicate that winterfat has supplanted shadscale along these transects. But it is also possible that these isotopic differences are due to fractionation during decomposition. If a sequence of organic matter transformation proceeds from 'humic acid' to 'fulvic acid', then the ^{13}C enrichment in the 'fulvic acid' fraction could simply be the result of microbial fractionation. Nissenbaum and Schallinger (1974) also found that the 'humic acid' fraction was consistently more negative ($\delta^{13}\text{C} = -28$ o/oo) than the 'fulvic acid' fraction ($\delta^{13}\text{C} = -25$ o/oo). They suggested that the 'fulvic acid' was isotopically similar to the dominant vegetation and hence it represented a low-molecular weight precursor in the process of polymerization of degraded plant material to 'humic acids' (Nissenbaum and Schallinger, 1974).

Because these investigators failed to measure the $\delta^{13}\text{C}$ value of the vegetation, their interpretation was challenged by Stout and Rafter (1978), who felt that it was more likely that the initial $\delta^{13}\text{C}$ value of the vegetation in Nissenbaum and Schallinger's study was closer to -28 o/oo and thus the 'humic acid' fraction was more similar to the isotopic composition of the vegetation. The enrichment of ^{13}C found in the 'fulvic acid' fraction would then be the result of soil fractionation (Stout and Rafter, 1978). The data from the present study would also support the notion that 'fulvic acid' is older; however, it is uncertain whether the ^{13}C enrichment in the 'fulvic acid' fraction is the result of soil fractionation or possibly a larger contribution of carbon derived from C_4 sources to the soil organic cycle in the past.

The data obtained in this study generally support the hypothesis that shadscale is increasing in importance in Curlew Valley, Utah. However, this conclusion is drawn only under the assumption that fractionation of stable carbon isotopes during decomposition occurs and is on the order of 3.0 o/oo. The uniformity of soil-root $\delta^{13}\text{C}$ differences in winterfat dominated areas is solid evidence in favor of this assumption. Conflicting, though questionable, interpretations would need to be based on the distribution of carbon isotopes with depth and the assumption that carbon enters the soil primarily from the soil surface. Radiocarbon dating, if not confounded by 'bomb' carbon, would help to clarify whether the large annual input of carbon through root turnover obliterates the normal depth-age relationship generally assumed for soils in mesic areas. In addition, such dating might help distinguish whether the 'fulvic acid' and

'humic acid' fractions represent significantly different stages in a decomposition continuum for these soils. At the present time, however, the most reasonable interpretation is that shadscale dominance is increasing in the salt-desert shrub communities of Curlew Valley, Utah.

LITERATURE CITED

- Antevs, E. 1952. Cenozoic climates of the Great Basin. *Geologische Rundschau* 40: 94-108.
- Bender, M.M. 1968. Mass spectrometric studies of carbon 13 variations in corn and other grasses. *Amer. J. Sci. Radiocarbon Suppl.* 10: 468-472.
- Bender, M.M. 1971. Variations in the $^{13}\text{C}/^{12}\text{C}$ ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. *Phytochem.* 10: 1239-1244.
- Boutton, T.W., G.N. Cameron and B.N. Smith. 1978. Insect herbivory on C_3 and C_4 grasses. *Oecologia* 36: 21-32.
- Braids, O.C. and R.H. Miller. 1975. Fats, waxes and resins in soil. pp. 343-368. *In*. J.E. Gieseking, ed. *Soil Components, Volume 1. Organic chemistry*. Springer-Verlag, New York.
- Branson, F.A., R.F. Miller, and I.S. McQueen. 1967. Geographic distribution and factors affecting the distribution of salt desert shrubs in the United States. *J. Range Man.* 20: 287-298.
- Bright, R.C. 1966. Pollen and seed stratigraphy of Swan Lake, southeastern Idaho: its relation to regional vegetational history and to Lake Bonneville history. *Tebiwa: the Journal of the Idaho State University Museum* 9: 1-47.
- Broecker, W.S. and P.C. Orr. 1958. Radiocarbon chronology of Lake Lahontan and Lake Bonneville. *Geol. Soc. Amer. Bull.* 69:1009-1032.
- Caldwell, M.M., R.S. White, R.T. Moore and L.B. Camp. 1977. Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C_3 and C_4 species. *Oecologia* 29: 275-300.
- Campbell, C.A., E.A. Paul, D.A. Rennie and K.J. McCallum. 1967. Factors affecting the accuracy of the carbon-dating method in soil humus studies. *Soil Sci.* 104: 81-85.
- Cronquist, A., A.H. Holmgren, N.H. Holmgren and J.L. Reveal. 1972. *Intermountain Flora, Vol. 1.* Hafner Publishing Company, New York. 270 pp.
- Degens, E.T., M. Behrendt, B. Gotthardt and E. Reppman. 1968. Metabolic fractionation of carbon isotopes in marine plankton—II. Data on samples collected off the coasts of Peru and Ecuador. *Deep-Sea Res.* 15: 11-20.
- DeNiro, M.J. and S. Epstein. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* 197: 261-263.

- DeNiro, M.J. and S. Epstein. 1978a. Carbon isotope evidence for different feeding patterns in two Hyrax species occupying the same habitat. *Science* 201: 906-908.
- DeNiro, M.J. and S. Epstein. 1978b. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* 42: 495-506.
- Eardley, A.J., V. Gvosdetsky and R.E. Marsell. 1957. Hydrology of Lake Bonneville and sediments and soils of its basin. *Geol. Soc. Amer. Bull.* 68: 1141-1201.
- Fernandez, O.A. and M.M. Caldwell. 1975. Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. *J. Ecol.* 63: 703-714.
- Fritts, H.C. 1971. Dendroclimatology and dendroecology. *Quaternary Res.* 1: 419-449.
- Fry, B., W-L. Jeng, R.S. Scalan and P.L. Parker. 1978a. $\delta^{13}\text{C}$ food web analysis of a Texas sand dune community. *Geochim. Cosmochim. Acta* 42: 1299-1302.
- Fry, B., A. Joern and P.L. Parker. 1978b. Grasshopper food web analysis: use of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. *Ecology* 59: 498-506.
- Gasto, J.M. 1969. Comparative autecological studies of Eurotia lanata and Atriplex confertifolia. Ph. D. dissertation, 278 pp. Logan, Utah: Utah State University.
- Gates, D.H., L.A. Stoddart and C.W. Cook. 1956. Soil as a factor influencing plant distribution on salt-deserts of Utah. *Ecol. Mono.* 26: 155-174.
- Goh, K.M., T.A. Rafter, J.D. Stout and T.W. Walker. 1976. The accumulation of soil organic matter and its carbon isotope content in a chronosequence of soils developed on aeolian sand in New Zealand. *J. Soil Sci.* 27: 89-100.
- Goh, K.M., J.D. Stout and T.A. Rafter. 1977. Radiocarbon enrichment of soil organic matter fractions in New Zealand soils. *Soil Sci.* 123: 385-391.
- Haines, E.B. 1976. Relation between the stable carbon isotope composition of fiddler crabs, plants and soils in a salt marsh. *Limn. Ocean.* 21: 880-883.
- Haines, E.B. 1977. The origin of detritus in Georgia salt marsh estuaries. *Oikos* 29: 254-260.

- Harper, K.T. 1959. Vegetational changes in a shadscale-winterfat plant association during twenty-three years of controlled grazing. M.S. Thesis. Brigham Young University. Provo, Utah.
- Harper, K.T. and G.M. Alder. 1970. Appendix I: The macroscopic plant remains of the deposits of Hogup Cave, Utah, and their paleoclimatic implications. pp. 215-240 In: (C. Melvin Aikens, ed.) Hogup Cave. Univ. of Utah Anthropol. Papers, No. 93.
- Herman, W.A., W.B. McGill and J.F. Dormaar. 1977. Effects of initial chemical composition on decomposition of roots of three grass species. Can. J. Soil Science 57: 205-215.
- Hoefs, J. 1973. Stable Isotope Geochemistry. Springer-Verlag. New York. 140 pages.
- Holmgren, R.C. and S.S. Hutchings. 1972. Salt desert response to grazing use. pp. 153-164. In: Wildland shrubs—their biology and utilization (C.M. McKell, J.P. Blaisdell, J.R. Goodin, eds.). USDA—Forest Service Gen. Tech. Rep. INT-1. Ogden, Utah.
- Holthausen, R.S. 1977. Seasonal course of root respiration in Atriplex confertifolia. M.S. Thesis. Utah State University. Logan, Utah. 54 pages.
- Hutchings, S.S. and G. Stewart. 1953. Increasing forage yields and sheep production on Intermountain winter ranges. USDA Circ. 925. 63 pages.
- Jenkinson, D.S. 1968. Studies on the decomposition of plant material in the soil. III. J. Soil Sci. 19: 25-39.
- Jenkinson, D.S. 1975. The turnover of organic matter in agricultural soils. Welsh Soils Discussion Group Report (Aberystwyth), 16: 91-105.
- Jenkinson, D.S. and J.H. Rayner. 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. Soil Sci. 123: 298-305.
- Keeling, C.D. 1958. The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas. Geochim. Cosmochim. Acta 13: 322-334.
- Keeling, C.D. 1961. The concentration and isotopic abundances of carbon dioxide in rural and marine air. Geochim. Cosmochim. Acta 24: 277-298.
- Kononova, M.M. 1966. Soil Organic Matter. Pergamon Press. Oxford. 544 pages.

- Lerman, J.C. 1975. How to interpret variations in the carbon isotope ratio of plants: biologic and environmental effects. pp. 323-335 In. R. Marcelle, ed. Environmental and biological control of photosynthesis. Dr. W. Junk Pubs., The Hague.
- Lowdon, J.A. and W. Dyck. 1974. Seasonal variations in the isotope ratios of carbon in maple leaves and other plants. Can. J. Earth Sci. 11: 79-88.
- Lukoshko, E.S. 1965. Changes in the chemical composition of peat-forming plants during decomposition of peat-forming layers under aerobic and anaerobic conditions. Vestis Akad. Navuk Belarusk. SSR. Ser: Khim Navuk 90 Chem. Abst. 64: 4212d (1966).
- Mehringer, P.J., Jr. 1967. Pollen analysis of the Tule Springs area, Nevada. pp. 105-128, In. H.M. Worthington and D. Ellis, eds. Nevada State Museum Anthropological Papers, No. 13.
- Mehringer, P.J., Jr. 1977. Great Basin late Quaternary environments and chronology. pp. 113-167, In. Don D. Fowler, ed. Models and Great Basin Prehistory. Desert Research Inst. Publ. in the Social Sciences No. 12.
- Minson, D.J., M.M. Ludlow and J.H. Troughton. 1975. Differences in the natural carbon isotope ratios of milk and hair from cattle grazing tropical and temperate pasture. Nature 256: 602.
- Mitchell, J.E., N.E. West and R.W. Miller. 1966. Soil physical properties in relation to plant community patterns in the shadscale zone of northwestern Utah. Ecology 47: 627-630.
- Moore, R.T. and M.M. Caldwell. 1972. Field use of thermocouple psychrometers in desert soils. pp. 165-169. In. R.W. Brown and B.P. van Haveren, eds. Psychrometry in water relations research. Utah Agric. Exp. Stn., Logan, Utah.
- Morrison, R.B. 1965. Quaternary geology of the Great Basin. pp. 265-285. In. The Quaternary of the United States. Princeton University Press. Princeton.
- Nissenbaum, A. and K.M. Schallinger. 1974. The distribution of the stable carbon isotope ($^{13}\text{C}/^{12}\text{C}$) in fractions of soil organic matter. Geoderma 11: 137-145.
- Norton, B.E. 1978. The impact of sheep grazing on long-term successional trends in salt desert shrub vegetation of southwestern Utah. Proc. First Int. Rangeland Cong. D.W. Hyder, ed. pp. 610-613.
- O'Brien, B.J. and J.D. Stout. 1978. Movement and turnover of soil organic matter as indicated by carbon isotope measurements. Soil Biol. Biochem. 10: 309-317.

- Ode, D.J. and L.L. Tieszen. 1978. Temporal production of C_3 and C_4 grasses in the Samuel H. Ordway Memorial Prairie. Proc. S.D. Acad. Sci. 57: 179.
- Oro, J., D.W. Nooner, A. Zlatkis, S.A. Wikstrom and E.S. Barhoorn. 1965. Hydrocarbons of biological origin in sediments about 2 billion years old. Science 148: 77-79.
- Park, R. and S. Epstein. 1960. Carbon isotope fractionation during photosynthesis. Geochim. Cosmochim. Acta 21: 110-126.
- Park, R. and S. Epstein. 1961. Metabolic fractionation of C^{13} and C^{12} in plants. Pl. Physiol. 36: 133-138.
- Parker, P.L. 1964. The biogeochemistry of the stable isotopes of carbon in a marine bay. Geochim. Cosmochim. Acta 28: 1155-1164.
- Paul, E.A., C.A. Campbell, D.A. Rennie and K.J. McCallum. 1964. Investigations on the dynamics of soil humus utilising carbon dating techniques. Trans. 8th Int. Cong. Soil Sci., Bucharest: 201-208.
- Persson, J. 1968. Biological testing of chemical humus analysis. Lantbrukshogsk Ann. 34: 81-217.
- Rafter, T.A. and J.D. Stout. 1970. Radiocarbon measurements as an index of the rate of turnover of organic matter in forest and grassland ecosystems in New Zealand. Nobel Symp. 12: 402-417.
- Rice, B. and M. Westoby. 1978. Vegetative responses of some Great Basin shrub communities protected against jackrabbits or domestic stock. J. Range Man. 31: 28-33.
- Skujins, J.J. and N.E. West. 1973. Nitrogen dynamics in stands dominated by some major cold deserts shrubs. US/IBP Desert Biome Res. Memo 73-75.
- Smith, B.N. 1975. $^{13}C/^{12}C$ natural abundance ratios as an indicator of changes in plant respiratory pathways. pp. 287-299. In: E.R. Klein and P.D. Klein, eds. Proc. Second Int. Conf. Stable Isotopes. USERDA Conf-751027.
- Smith, B.N. and C.R. Benedict. 1974. Carbon isotopic ratios of chemical constituents of Panicum maximum L. Pl. & Cell Physiol. 15: 949-951.
- Smith, B.N. and S. Epstein. 1971. Two categories of $^{13}C/^{12}C$ ratios for higher plants. Pl. Physiol. 47: 380-384.
- Smith, B.N. and B.S. Jacobsen. 1976. $^2H/^1H$ and $^{13}C/^{12}C$ ratios for classes of compounds isolated from potato tuber. Pl. & Cell Physiol. 17: 1089-1092.

- Smith, B.N., J. Oliver and C. McMillan. 1976. Influence of carbon source, oxygen concentration, light intensity and temperature on $^{13}\text{C}/^{12}\text{C}$ ratios in plant tissues. Bot. Gaz. 137: 99-104.
- Snyder, C.T. and W.B. Langbein. 1962. The Pleistocene lake in Spring Valley, Nevada, and its climatic implications. J. Geophys. Res. 67: 2385-2394.
- Springer, V. and A. Lehner. 1952a. Decomposition and the synthesis of humus by aerobic and anaerobic decomposition of organic substances important in agriculture and forestry. 1. Z. Pflernahr. Dung. 58: 193-231.
- Springer, V. and A. Lehner. 1952b. Decomposition and the synthesis of humus by aerobic and anaerobic decomposition of organic substances important in agriculture and forestry. 2. Z. Pflernahr. Dung. 59: 1-27.
- Stewart, G., W.P. Cottam and S.S. Hutchings. 1940. Influence of unrestricted grazing on northern salt desert plant associations in western Utah. J. Agric. Res. 60: 289-316.
- Stewart, G. and S.S. Hutchings. 1936. The point-observation-plot (square foot density) method of vegetation survey. J. Amer. Soc. Agron. 28: 714-722.
- Stout, J.D. and B.J. O'Brien. 1972. Factors affecting radiocarbon enrichment in soil and the turnover of soil organic matter. pp. E13-E26. In: T.A. Rafter and T. Grant-Taylor, eds. Proc. 8th Int. Conf. Radiocarbon Dating. Royal Society of New Zealand. Lower Hutt.
- Stout, J.D. and T.A. Rafter. 1978. The $^{13}\text{C}/^{12}\text{C}$ isotopic ratios of some New Zealand tussock grassland soils. pp. 75-83. In: B.W. Robinson, ed. Stable Isotopes in the Earth Sciences. DSIR Bull. 220. Wellington, New Zealand.
- Stout, J.D., T.A. Rafter and J.H. Troughton. 1975. The possible significance of isotopic ratios in palaeoecology. pp. 279-286. In: R.P. Suggate and M.M. Cresswell, eds. Quaternary Studies. The Royal Society of New Zealand.
- Stuiver, M. 1978. Atmospheric carbon dioxide and carbon reservoir changes. Science 199: 253-258.
- Stutz, H.C. 1978. Explosive evolution of perennial Atriplex in western North America. Great Basin Nat. Mem. 2: 161-168.
- Thayer, C.W., P.J. Parker, M.W. LaCroix and B. Fry. 1978. The stable carbon isotope ratio of some components of an eelgrass, Zostera marina, bed. Oecologia 35: 1-12.

- Tidwell, W.D., S.R. Rushforth and D. Simper. 1972. Evolution of floras in the Intermountain region. pp. 19-39. In. Intermountain Flora, Vol. 1. Hafner Pubs. Co. Inc., New York.
- Tieszen, L.L., D. Hein, S.A. Qvortrup and J.H. Troughton. 1979b. Use of $\delta^{13}\text{C}$ values to determine vegetation selectivity in East African herbivores. *Oecologia* 37: 351-359.
- Tieszen, L.L., M.M. Senyimba, S.K. Imbamba and J.H. Troughton. 1979a. The distribution of C_3 and C_4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* 37: 337-350.
- Troughton, J.H. 1971. Aspects of the evolution of the photosynthetic carboxylation reaction in plants. pp. 124-129. In. M.D. Hatch, C.B. Osmond and R.O. Slatyer, eds. *Photosynthesis and Photorespiration*. John Wiley and Sons, Inc., New York.
- Troughton, J.H. 1972. Carbon isotope fractionation by plants. pp. E39-E58. In. T.A. Rafter and T. Grant-Taylor, eds. *Proc. 8th Int. Conf. Radiocarbon Dating*. Royal Society of New Zealand. Lower Hutt.
- Troughton, J.H. and K.A. Card. 1975. Temperature effects on the carbon isotope ratio of C_3 , C_4 and Crassulacean Acid Metabolism (CAM) plants. *Planta* 123: 185-190.
- Troughton, J.H., J.D. Stout and T. Rafter. 1974b. Long-term stability of plant communities. *Carn. Inst. Wash. Yearbook* 73: 838-845.
- Troughton, J.H., P.V. Wells and H.A. Mooney. 1974a. Photosynthetic mechanisms and paleoecology from carbon isotope ratios in ancient specimens of C_4 and CAM plants. *Science* 185: 610-612.
- Turfitt, G.E. 1943. The microbiological degradation of steroids. 1. The sterol content of soil. *Biochem. J.* 37: 115-117.
- VanDevender, T.R. and G.W. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. *Science* 204: 701-710.
- Waksman, S.A. and K.R. Stevens. 1929. Contribution to the chemical composition of peat. V. The role of microorganisms in peat formation and decomposition. *Soil Sci.* 28: 315-340.
- Waksman, S.A., F.G. Tenny and K.R. Stevens. 1928. The role of microorganisms in the transformations of organic matter in forest soils. *Ecology* 9: 126-144.
- Weikie, G.W. and M.M. Calawell. 1970. Leaf anatomy of species in some dicotyledon families as related to the C_3 and C_4 pathways of carbon fixation. *Can. J. Bot.* 48: 2135-2146.

- West, N.E. 1979. Survival of eight salt desert plants in southwestern Utah. *J. Range Man.* In press.
- West, N.E. and J.J. Skujins. 1978. Summary, conclusions and suggestions for further research. pp. 244-253. In. N.E. West and J.J. Skujins, eds. *Nitrogen in Desert Ecosystems*. US/IBP Synthesis Ser. 9. Dowden, Hutchinson and Ross, Inc. Stroudsburg, Pa.
- Wilson, A.T. 1978. Pioneer agriculture explosion and CO_2 levels in the atmosphere. *Nature* 273: 40-41.
- Wilson, A.T. and M.J. Grinstead. 1977. $^{12}\text{C}/^{13}\text{C}$ in cellulose and lignin as palaeothermometers. *Nature* 265. 133-135.
- Wright, H.E., Jr. 1971. Late Quaternary vegetational history of North America. pp. 425-464. In. K.K. Turekian, ed. *Late Cenozoic Glacial Ages*. Yale University Press. New Haven.
- Young, J.A., R.A. Evans and J. Major. 1977. Sagebrush steppe. pp. 763-796. In. M.G. Barbour and J. Major, eds. *Terrestrial vegetation of California*. John Wiley and Sons, New York.

APPENDIXES

Appendix A

Carbon Isotope Ratios of Samples from Transect #2

Table 4. $\delta^{13}\text{C}$ values of litter, roots and soils from transect #2. Sample combustions and isotope determinations have a combined standard deviation of 0.1 o/oo. Vegetation cover key is: W = winterfat, S = shadscale and W/S = mixed winterfat and shadscale.

Core #	Vegetation Cover	Depth (cm)	$\delta^{13}\text{C}$ -litter	$\delta^{13}\text{C}$ -roots	$\delta^{13}\text{C}$ -soils
1	W	surface	-23.9		
		0-15		-25.5	-22.0
		15-30		-24.4	-21.6
		30-45		-25.2	-21.3
2	W	surface	-22.4		
		0-15		-23.4	-21.8
		15-30		-23.5	-20.9
		30-45		-25.2	-20.8
3	W/S	surface	-25.1		
		0-15		-24.5	-21.9
		15-30		-24.9	-21.3
		30-45		-24.3	-20.6
4	W/S	surface	-21.8		
		0-15		-22.8	-21.2
		15-30		-23.4	-20.7
		30-45		-23.4	-20.1
5	S	surface	-16.6		
		0-15		-23.6	-21.3
		15-30		-23.0	-21.0
		30-45		-22.2	-20.6

Appendix B

Carbon Isotope Ratios of Samples from Transect #3

Table 5. $\delta^{13}\text{C}$ values of litter, roots and soils from transect #3. Sample combustions and isotope determinations have a combined standard deviation of 0.1 o/oo. Vegetation cover key is W= winterfat, S=shadscale and W/S= mixed winterfat and shadscale.

Core #	Vegetation Cover	Depth (cm)	$\delta^{13}\text{C}$ -litter	$\delta^{13}\text{C}$ -roots	$\delta^{13}\text{C}$ -soils
1	W	surface	-22.2		
		0-15		-25.9	-23.1
		15-30		-25.4	-22.1
		30-45		-23.6	-21.4
2	W/S	surface	-22.8		
		0-15		-24.0	-20.7
		15-30		-23.0	-19.9
		30-45		-21.7	-19.3
3	W	surface	-24.1		
		0-15		-24.2	-21.8
		15-30		-24.4	-20.8
		30-45		-23.3	-20.5
4	S	surface	-20.1		
		0-15		-23.1	-21.0
		15-30		-19.6	-20.3
		30-45		-18.5	-19.6
5	S	surface			
		0-15		-24.9	-20.9
		15-30		-23.3	-19.9
		30-45		-21.4	-19.5
		45-65		-17.6	-18.6
		65-75		-16.7	-18.3